Chapter 8

Cortical Visual Areas of the Temporal Lobe
Three Areas in the Macaque

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1. Introduction

Primates are very visual animals. Thus, it is not surprising that over half of their cerebral cortex is devoted primarily to visual function (67). In this essay, we will consider three rather different cortical visual areas, all of which lie within the temporal lobe of the macaque, viz., the Middle Temporal Area (or MT), the Inferior Temporal Area (or IT) and the Superior Temporal Polysensory Area (or STP). Their locations are shown in Fig. 8.1.
Fig. 8.1. The small drawing shows a lateral view of the cerebral hemisphere of the macaque. The larger drawings are traced from a photograph of a brain, in which the superior temporal sulcus (STS), the lunate sulcus and the inferior occipital sulcus (INF. OCC. S.) were opened up to show their banks and fundi. The lower drawing indicates the location of the areas discussed in this paper. The area shown in grey is additional visually responsive prestriate cortex. ANT. B., anterior bank; IT, inferior temporal cortex; MT, middle temporal area; POST. B., posterior bank; PP, posterior parietal cortex; STP, superior temporal polysensory area.
For each area we will consider (a) its location and architectonic characteristics, (b) the visual properties of its neurons, (c) its afferents and efferents and (d) the behavioral effects of its removal. Then we will suggest that the various extrastriate cortical visual areas may be divided into three functional classes and that each of the three temporal areas discussed are representative of one of these classes.

2. The Middle Temporal Area (MT)

2.1. Location and Architectonics

MT lies in the floor and adjacent portion of the lower bank of the caudal third of the superior temporal sulcus as shown in Figs. 8.2 and 8.3 (22, 23, 46, 65, 67). It falls within cytoarchitectonic area OA of von Bonin and Bailey (68) and area 19 of Brodmann (10); thus, it is a portion of prestriate cortex. In fiber-stained sections, it is readily distinguishable from the adjacent cortex by heavy myelination in layers four through six.

Although this area is located at the junction of the occipital, temporal and parietal lobes of the macaque, it has been called the Middle Temporal area (MT) (1, 46, 66, 67, 70) because on several grounds it appears homologous to an area designated MT in other primates (1, 2, 3, 63, 66). In these species, MT is indeed in the middle of the temporal lobe. In the macaque, this area has also been called the “STS-movement area” (77, 81, 82), and the “striate-projection zone in the superior temporal sulcus” (23, 65).

2.2. Neuronal Properties

MT neurons respond only to visual stimuli. Their receptive fields are organized to provide a topographic representation of the contralateral visual hemifield (22, 23, 46, 65, 67). The visuotopic organization is similar to that of striate cortex, that is, a first-order transformation of the visual field. The representation of the vertical meridian partially surrounds the area and lies near the bottom of the lower bank of the superior temporal sulcus (STS). The representation of the horizontal meridian runs across the floor of STS, the upper visual field being anterior and the lower visual field posterior (see Figs. 8.2 and 8.3). As in striate cortex, the representation of the central visual field is greatly magnified. Receptive field size increases strikingly with eccentricity so that receptive fields with
Fig. 8.2. Progression of receptive fields in MT. A, lateral view of hemisphere showing level of cross section. B, cross-section showing the location of the electrode penetrations and the portion of the superior temporal sulcus (STS) enlarged below. C, section through the superior temporal sulcus showing the location of MT (heavily dashed line between arrows) and of recording sites within MT (1–6) and in the surrounding areas. The fourth cortical layer (thinner dashed line) is also shown and the projection of the recording sites onto it. D, location of the receptive field centers re-
Fig. 8.2. (continued)

corded at sites 1–9. Note that, as one moves from site 1 to site 6, the receptive field centers move systematically from the center of gaze into the periphery. Between site 6 and 7 the myeloarchitecture changes; sites 7–9 are outside of MT, and from site 7 to site 9 the field centers move towards the horizontal meridian. E, receptive fields recorded at sites 1–6. Note the rapid increase in receptive field size with eccentricity (22).
FIG. 8.3. Visuotopic organization of MT. A, lateral view of hemisphere showing location of sections used to construct an unfolded map of the portion of the STS that includes MT. Wires were bent to conform to layer 4 of each section and then were attached with scaled cross pieces to form a three-dimensional model of the relevant region of STS. The model was then flattened by cutting the minimum number of cross pieces to form a two-dimensional surface. B, section 7 showing MT (heavy dashed line) and location of upper bank (UB), fundus (F) and lower bank (LB) of STS. (This section was shown in Fig. 8.2.) C, map of visual hemifield showing meridians and isoeccentricity lines. D, tracing of flattened model constructed from the sections. The locations of the receptive fields were plotted on the tracing. On the basis of the coordinates of the receptive field centers, the vertical meridian (large dots), the horizontal meridian (squares) and the isoeccentricity lines (dashed) were drawn. The dotted lines show the discontinuities produced by flattening the three dimensional model. The numbered lines (1–9) correspond to the coronal sections shown in A (22).
their centers 10–20° from the fovea are often so large that their med-
dial borders are on or near the vertical meridian (Fig. 8.2E). Per-
haps because of the larger receptive fields of its neurons and its rel-
atively small total area, the visuotopic organization of MT is
somewhat cruder than that of either V I (V I), or V2 (V II) (22, 23).

Unlike neurons in other prestriate areas, a large proportion of
MT neurons are sensitive to the direction of movement of a stimu-
lus, but are relatively insensitive to form, orientation, size or color
(46, 77, 80, 81, 82). Some MT neurons apparently respond to
changing disparity or to stimuli with expanding or contracting
contours (78); these units may signal movement in depth. Finally,
MT neurons, as in other prestriate areas, generally respond equally
to stimulation of either eye (81).

2.3. Anatomical Connections

MT receives a topographically organized projection from striate cortex (65, 70); thus, it is a “striate-recipient” area, as is V2 (V II) (74).
MT also receives projections from V2 (V II) (79) and from the ante-
rior parts of the inferior and lateral pulvinar (8). Since these por-
tions of the pulvinar apparently receive a tectal projection (7, 8), MT
may be the site of converging inputs from the geniculostriate and
tectofugal systems.

MT projects back to striate cortex in a topographically organ-
ized fashion (70). Otherwise the targets of MT axons have not been
investigated in the macaque.

2.4. Behavioral Effects of Removal

Since the location of MT in the macaque has only recently been de-
scribed, there are very few data on the effects of its selective re-
moval. MT lesions do not seem to impair acquisition or retention of
visual pattern discrimination problems (4, 64). However, they do
impair a monkey’s ability to pick a small food pellet out of a narrow
slot and to detect and grasp a loose peanut mounted on a back-
ground of fixed peanuts (4). These results suggest that MT, unlike
IT (see next section), may not be directly involved in visual pattern
learning, but rather in other visual functions, perhaps of a
visuomotor or strictly sensory nature. A similar suggestion has
been made by Wilson and her colleagues (72).
3. Inferior Temporal Cortex (IT)

3.1. Location and Architectonics

IT lies on the inferior convexity of the temporal lobe. It extends from about 6 mm anterior to the ascending portion of the inferior occipital sulcus to within a few millimeters of the temporal pole and from the floor of the superior temporal sulcus to the depths of the occipitotemporal sulcus (21). IT corresponds closely to cytoarchitectonic area TE, as defined by von Bonin and Bailey and others (21, 62, 68).

3.2. Neuronal Properties

IT neurons respond only to visual stimuli. Unlike V1 (V I), V2 (V II) and MT, inferior temporal cortex is not visuotopically organized (21, 27, 33). Rather, throughout IT, receptive fields almost always include the center of gaze and in a majority of cases extend well across the vertical meridian into both visual half-fields (Fig. 8.4). IT receptive fields are particularly large for receptive fields that include the center of gaze; the median receptive field size is approximately 25 × 25° (21,27,29,33). Unlike neurons in striate cortex, most IT neurons respond better to complex objects than to slits of light or edges (18, 33). The majority appear selective for features of objects such as their shape, texture or color. Responses of one such neuron are shown in Fig. 8.5. A few IT units appear selective for specific objects such as hands or faces. The stimulus selectivity of a given IT neuron is similar throughout its large receptive field (32, 33). That is, they show stimulus equivalence across retinal translation. These properties of IT neurons indicate that they play a role in analyzing the global aspects of a complex object such as its shape, rather than in analyzing local features such as the retinal locus of edges and borders.

Within IT, there are two regions that have larger receptive fields and are cytoarchitectonically distinguishable from the rest of IT. The first is in the most rostral part and the second lies along the dorsal border of IT in STS (21).

3.3. Anatomical Connections

The visual properties of IT units depend on a multisynaptic cortico-cortical input from striate cortex (58). Striate cortex does not pro-
Fig. 8.4. Receptive fields of single neurons on a series of penetrations through inferior temporal cortex. Receptive fields are represented by best-fitting rectangles. In some cases, receptive field borders extending beyond the 60 × 60° tangent screen were not determined and are represented by dashed lines; receptive fields smaller than 8° were all located at the center of gaze and are shown as dots. The meridians of the visual field are represented by vertical and horizontal lines. Note that all the receptive fields include the center of gaze and that many fields extend far into the ipsilateral hemifield. Although neurons with similar receptive fields tend to cluster, there is no sign of any visuotopic organization. The inset shows the location of the section on a lateral view of the brain and the portion of the section enlarged in the main figure. The scale applies to the receptive field dimensions.(21)
through the window. Each of the histograms is based on five interleaved trials. Orientation and direction of movement were not relevant (18).
ject directly to IT cortex (16, 20, 41, 74). Rather, striate cortex projects to V2 (V II) and other striate-recipient prestriate areas. These project to more anterior prestriate areas (including Zeki's V4 complex) (20, 75). Finally, these anterior prestriate areas project directly to IT cortex (Fig. 8.6) (20). Thus, there are at least two processing stages between striate and IT cortex. In addition to this ipsilateral route, IT receives visual information from contralateral anterior prestriate cortex and the contralateral IT cortex by way of both the splenium and the anterior commissure (20, 30, 52, 53, 76). IT cortex also receives projections from visually responsive areas in lateral frontal cortex (40) and the posterior portion of the lateral pulvinar (8).

IT cortex projects to a variety of cortical and subcortical sites. IT projects to lateral frontal cortex, anterior prestriate cortex and the posterior part of the lateral pulvinar (40, 41, 71). IT cortex also projects to the STS polysensory area and parahippocampal region (40, 41) and to several subcortical sites including the amygdala, the tail of the caudate nucleus, the dorsomedial nucleus of the thalamus and the deep layers of the superior colliculus (71).

3.4. Behavioral Effects of Removal

Bilateral removal of inferior temporal cortex produces a severe deficit in visual discrimination learning. This deficit occurs in the absence of any change in sensory status; visual acuity, a variety of other psychophysical thresholds and the integrity of the visual fields all remain normal after IT lesions, as does discrimination learning in other modalities than the visual (15, 26, 27).

The discrimination impairment after IT lesions is both in postoperative acquisition and postoperative retention of visual discrimination tasks. It occurs with a great variety of discriminanda, such as stimuli differing in pattern, shape, size, brightness and color and with a variety of training methods. There are several conditions under which the impairment may be reduced or absent: when the task is very simple; when the discriminanda are patterns differing in orientation by 90 or 180°; when the animals receive extensive preoperative training and when the lesions are made in infancy (26, 28).

Different partial lesions of IT cortex produce somewhat different deficits. The deficits after posterior IT lesions have been characterized as perceptual in nature, whereas the more anterior ones seem to be mnemonic (14, 27, 45, 48).
FIG. 8.6. Distribution of labeled cells in occipital and temporal cortex following injections of the retrograde tracer horseradish peroxidase (HRP) into inferior temporal cortex. In the lateral reconstructions, × indicates the sites of the iontophoretic injections and the shaded area indicates the area of spread of HRP. The relative density of labeled cells is indicated by dots and arrows delimit where labeled cells were found in a bank of a major sulcus. Labeled cells were also found in both banks of the anterior middle temporal sulcus and in the occipitotemporal sulcus, mainly in the lateral bank. In the coronal sections, the black areas indicate the sites of the injections, the hatched areas indicate the spread of HRP and each dot represents an individual labeled cell. Note that HRP-labeled cells were found throughout IT itself (outside the injection area), but were not found in the polysensory areas that surround IT dorsally, anteriorly and ventrally. Posterior to IT, labeled cells were found in the anterior parts of prestriate cortex. This prestriate region that projects to IT is mainly devoted to the central visual field and does not include any of the prestriate areas that receive direct projections from striate cortex, such as MT or V2 (20).
4. Superior Temporal Polysensory Area (STP)

4.1. Location and Architectonics

The area we have termed the superior temporal polysensory area lies chiefly in the upper bank of the middle and rostral portions of the superior temporal sulcus immediately dorsal to IT (11, 12, 21). Anteriorly it crosses the floor of STS and extends onto the lateral surface at the temporal pole. It corresponds approximately to Area T3 defined by Jones and Burton (39) on grounds of architectonics and pulvinar afferents.

4.2. Neuronal Properties

Virtually all the neurons in STP are responsive to visual stimuli. However, in contrast to both MT and IT, almost half the neurons in STP are also responsive to auditory or somesthetic stimuli and many respond to stimulation in all three modalities (Figs. 8.7 and

![Bar chart showing frequency of STP neurons responsive to different sensory modalities. The percentages are based on 382 neurons tested for visual (VIS), auditory (AUD), and somesthetic (SOM) responses. UNRESP, unresponsive to visual, auditory, and somesthetic stimuli (11).]
Fig. 8.8. Poststimulus time histograms showing the responses of three STP neurons to a visual stimulus, to a click and to a mechanical tap on the bottom of the foot. The visual stimulus for the upper and middle histograms was a vertical slit of light and for the bottom histogram a color slide of a monkey's face. The vertical scale in this and subsequent histograms represents the number of impulses per second. The horizontal lines indicate the presentation of the visual stimuli and the arrows the presentation of the auditory and somesthetic ones (11).

8.8). It was this multimodal responsivity that led us to name the area the "superior temporal polysensory area" (11, 12).

The visual receptive fields in STP are extraordinarily large, even when compared with those in inferior temporal cortex (Fig. 8.9). The majority of them extends into the monocular crescent of both eyes; the median value for the contralateral extent is 80°, for the ipsilateral extent 70°, for the upperward extent 50° and for the downward extent 55°. Thus, for most STP units the receptive field approaches the size of the monkey's visual field. Obviously, this
Fig. 8.9. Typical visual receptive field of a STP neuron (upper) and responses (lower) to a stimulus moved along each of the meridians in the direction indicated by the arrows. In the receptive field plot, the horizontal and vertical lines represent the meridians. The stimulus was a 5° white square moving at approximately 35°/s along a circular path around the animal's head. The scale under each trace indicates the location of the stimulus. Only the contralateral eye was stimulated. In each case the stimulus began moving outside the visual field, moved through the receptive field and then left the visual field. C, contralateral; I, ipsilateral; L, lower; U, upper (11).
precludes any type of visuotopic organization. Responses are usually similar throughout the receptive field and are not more vigorous at the center of gaze, as is the case for IT neurons.

In contrast to IT units (but more similar to MT units), the majority of STP units is not sensitive to the size, shape, orientation, color or contrast of the visual stimulus. STP units respond particularly well to moving stimuli and about half show one of three types of direction selectivity. One class of units has conventional or uniform direction preferences, such as leftward or downward throughout the receptive field. Another class of units has an unusual, nonuniform type of direction preference. About half of the units in this class respond to any movement directed away from the fovea (Fig. 8.10). The other half prefers stimulus movement towards the fovea. Finally, a third class responds to stimulus motion in depth: to movement either toward or away from the animal (Fig. 8.11).

A minority of STP units appears particularly sensitive to monkey and human faces (Fig. 8.12). Similar units have been described in both inferior temporal (18, 33) and lateral frontal cortex (56).

### 4.3. Anatomical Connections

STP receives afferents from inferior temporal cortex, superior temporal auditory association cortex and posterior parietal cortex (38, 40, 41, 62). These connections may be sources of its visual, auditory and somesthetic sensitivity, respectively. It also receives afferents from a variety of other cortical and subcortical areas, including cingulate cortex, the parahippocampal region, the frontal eye fields, the amygdala and the medial pulvinar (38, 39). The connections with both the frontal eye fields and posterior parietal cortex are reciprocal ones (17, 47).

As mentioned previously, the visual responses of IT neurons are dependent on the corticocortical input they receive from striate cortex (58). This is apparently also true of V2 (V II) neurons (60). Surprisingly, this is not true of STP neurons (19). Following unilateral striate lesions, over two-thirds of STP neurons remain visually responsive in the "cortically blind" half-field. However, in these units, response strength, receptive field size and direction specificity are all reduced in the half-field contralateral to the lesion. Preliminary evidence indicates that the addition of a superior colliculus lesion to the striate cortex lesion eliminates this visual responsiveness. Thus, apparently both striate cortex and the superior colliculus contribute to the visual properties of STP neurons. After total bilateral removal of striate cortex, macaques retain or recover an impressive degree of visually guided behavior (e.g., 37, 50,
Fig. 8.10. Responses of a STP unit selective for stimulus movement away from the center of gaze. The histograms show the responses to a $5^\circ \times 3^\circ$ stimulus moving on a circular path around the animal's head along the horizontal meridian at $22^\circ$/s or the vertical meridian at $15^\circ$/s. The arrows indicate the direction of stimulus movement. Only the contralateral eye was stimulated (11).

69). It is possible that the visual functions of STP that remain after striate lesions contribute to this residual vision.

4.4. Behavioral Effects of Removal

In one of the few studies of lesions largely confined to STP, no deficits were found in visual discrimination learning (55). However, these animals did have a severe deficit in a visuospatial task requiring them to "unstring" a piece of food from a wire with multiple bends (55) and in a multimodal task involving a visual–auditory association (54).
Fig. 8.11. Responses of a STP unit selective for stimulus movement away from the animal. The stimulus was a color photograph of a monkey face moving at approximately 20 cm/s along the paths indicated by the arrows. The dashed lines indicate the mean spontaneous rate in the interstimulus intervals. Note that movement toward the animal reduces the rate of firing. One eye was occluded as shown on the left. The receptive field extended approximately 65° into each visual hemifield. The ordinate is in spikes/s (11).

5. An Hypothesis: Three Classes of Extrastriate Visual Areas

The middle temporal area (MT), inferior temporal cortex (IT) and the superior temporal polysensory area (STP) represent only a minority of the extrastriate visual areas devoted primarily or exclusively to visually guided behavior. For most of the extrastriate visual areas, in contrast to striate cortex, we do not have a complete description of their inputs and outputs, we know little about the behavioral effects of their selective removal and their neuronal properties have only been examined under a restricted set of stimulus and behavioral conditions. Even at this early stage, however, it may be helpful to try to group them into functional classes. The extrastriate visual areas appear to fall into three classes and, it will be argued, each of the temporal areas discussed in this essay exemplifies one of these classes.
Fig. 8.12. Responses of an STP unit that responded better to pictures of faces than to a variety of other stimuli. Removing the eyes or representing the face as a caricature reduced the response. Cutting the picture into sixteen pieces and re-arranging the pieces eliminated the response. The stimuli represented on the left were traced from a color photograph (monkey face), black and white photographs (human face) or drawings (caricature and random bars) which were swept across the fovea at 10°/s. The stimuli represented on the right were traced from color slides which were projected centered on the fovea for 3 s, indicated by the horizontal bars. All of the unit records are representative ones chosen from a larger number of trials. The receptive field is illustrated on the lower right (11).
The first class consists of the various prestriate areas within
cytoarchitectonic areas OB and OA. This class may be defined as
being exclusively visual and visuotopically organized, i.e., its recep-
tive fields are arranged to form a spatial representation of the con-
tralateral visual field. Although varying in their visual topography,
the members of this class are characterized, like striate cortex, by a
magnification of the central portion of the visual field. They receive
either direct input from striate cortex or direct input from a striate-
recipient area (66, 81, 82). Preliminary neurophysiological evi-
dence indicates that neurons in some of these areas may be rela-
tively specialized for the analysis of such stimulus features as
direction of movement and size (1, 36, 81, 82). MT is an example of
this first class as are V2 (V II) and V3 (V III).

The second class consists of inferior temporal cortex. This class
may be defined as being exclusively visual and not visuotop-
ically organized (21, 31, 33); the receptive fields almost always in-
clude the center of gaze and usually extend well into both visual
half-fields. This class receives input from nonstriate-recipient
members of the first class. Inferior temporal neurons are usually
sensitive to several stimulus dimensions and often have highly
complex trigger features. Although this class consists only of infe-
rior temporal cortex, it appears subdividable in terms of its cytoar-
chitectonics, its connections, its neuronal properties and the be-
havioral effects of partial lesions (17, 21, 26, 45).

The third class may be defined as being not exclusively visual
and having little or no visuotopic organization. It is characterized
by having neurons that usually (a) have very large visual receptive
fields, (b) are not sensitive to form or color per se and (c) are sensi-
tive to auditory or somesthetic stimulation or are related to motor
acts or both. This class includes the superior temporal polysensory
area described above, the frontal eye fields (area 8), posterior pariet-
al cortex (area 7), and perhaps the parahippocampal region (12,
21, 49, 51, 57). Furthermore, the members of this class are recipro-
cally connected with each other.

Although all three classes of visual areas receive projections
from both the geniculostriate and tectofugal visual pathways, only
the geniculostriate system appears crucial for the visual properties
of the first two classes (19, 25, 42, 60). By contrast, the superior
colliculus appears intimately involved in the functions of the third
class.

What may be the functions of these three classes of visual
areas?

Removal of inferior temporal cortex, the second class, in both
man and monkey produces impairments in visual perception and
visual memory in the absence of any visuosensory changes (26, 27).
These results indicate that the second class is involved in pattern perception and recognition. The fact that IT neurons are particularly concerned with the center of gaze, have complex trigger features and show stimulus equivalence across retinal translation (18, 32, 61) further supports this view.

Several lines of evidence suggest that the third class of visual areas is particularly involved in relating visual stimuli to movement, that is, in spatial orientation and visuomotor (especially oculomotor) mechanisms. Posterior parietal lesions impair spatial orientation, visuococonstructive skills, visually guided locomotion and reaching and they produce various neglect and inattention symptoms; posterior parietal neuronal activity is correlated with both eye movements and orienting to and reaching toward visual stimuli (34, 35, 42, 51, 57). Frontal eye field lesions produce both visual neglect and deficits on spatial tasks and its neurons discharge in relation to eye movements (9, 43, 44, 59, 73). STP lesions produce both a neglect syndrome and visuomotor disturbances; the very large receptive fields of its neurons and their unusual directional selectivities suggest a role in spatial orientaton (11, 12, 54, 55). These three "third class" areas have two other properties that further suggest that they form a system for linking sensory input with action. The first is that they are closely associated with the superior colliculus and the superior colliculus is a sensory-motor structure concerned with oculomotor, orientation and localization functions. The second is that, like the superior colliculus, neurons in all three areas respond to nonvisual as well as visual stimuli (12, 49, 51). This may reflect the fact that orientation and localization, although especially visual in primates, are actually supramodal functions.

Areas of the first class, the prestriate areas, are at an earlier stage of visual processing than the other two classes. They appear concerned with the analysis of specific visual features at a specific retinal locus (13, 81). Large lesions of prestriate cortex that include the foveal representations of several prestriate areas produce visual learning deficits even more severe than those following IT lesions (27). The converging outputs of the various prestriate areas may provide the basis upon which the second class elaborates its pattern recognition functions and the third class its visuomotor functions.

Finally, it should be noted that we have been concerned exclusively with cortical visual mechanisms. However, there are subcortical mechanisms also concerned with stimulus analysis and visuomotor function. For example, the pulvinar projects to all three classes of cortical visual areas and itself contains several visuotopically organized areas and several classes of stimulus fea-
ture analyzers (5, 6, 8, 24). Certainly, an understanding of the mechanisms of visually guided behavior will require not only understanding the cortical visual areas but also their interaction with subcortical visual structures.

Acknowledgments

We would like to thank A. P. B. Sousa, V. Ingalls and G. Barber for their critical comments, K. Aragão de Carvalho for help with the figures and B. Pinkham for typing.

Preparation of this chapter was supported by NIH Grant MH-19420 and NSF Grant BNS 79-05589. CB was supported by NIH Grant NS-05804, RD by NSF Grant SPI-7914804 and RG by a grant from Brazil, CNPq 1112.1003/77.

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